

## DEW-DRINKING BY MALE MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* (L.)

DENNIS FREY, ROBERT ROMAN AND LINDSAY MESSETT

Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407, USA

**ABSTRACT.** We examined the early morning activity of overwintering monarch butterflies at a central coast California site during their period of “mass-mating” from mid-January to mid-March in 1998 and 1999. The first year of the study took place during El Niño weather when regional precipitation was approximately 50% greater than normal. The second year occurred during La Niña conditions with approximately 15% less precipitation than normal. On “rain-free” mornings many of the butterflies left aggregations and flew to an adjacent meadow where they landed on grass and drank from dew droplets. Males were much more likely to make morning meadow visits than females and such males had 6.7% higher body moisture than males that remained in the clusters. The rate of male meadow use increased seasonally both years and males were frequently seen attempting to mate following dew-drinking meadow visits. Early morning meadow-males resembled males attempting to mate in the morning more than males that were not mating, i.e., that remained in aggregations. Meadow-males were smaller, had relatively smaller dry-weight abdomen mass, and had more wing damage in addition to their greater moisture content. Variation in local solar radiation, wind speed and evapotranspiration during the previous 24 h was positively associated with early morning meadow use by both males and females. Male mating effort during the previous day was positively associated with early morning dew-drinking by males but not females. Three hypotheses regarding dew-drinking activity are considered. The results are consistent with two perspectives: dew drinking results from dehydrating activity such as courtship and spermatophore transfer during the previous day and/or it represents strategic male behavior in anticipation of “need” for future reproductive effort.

**Additional key words:** *Danaus plexippus*, dew-drinking, mating effort, dehydration, El Niño, La Niña.

Each fall monarch butterflies, *Danaus plexippus* (L.), migrate from an extensive late summer breeding range in North America to geographically restricted overwintering habitats (Brower & Malcolm 1991). Monarchs from eastern breeding populations overwinter in several mountainous areas dominated by Oyamel fir forests near Mexico City (Urquhart & Urquhart 1978, Brower 1985, Calvert & Brower 1986). Those originating west of the Rocky Mountains overwinter at wooded sites located along the Pacific Ocean between Bolinas, California and Ensenada, Mexico (Sakai & Calvert 1991, Lane 1993).

The general eco-region macroclimate where these sites are located, along with local topography and vegetation, provide microclimate conditions favorable for monarch overwintering (Brower et al. 1977, Calvert et al. 1982). Conditions thought to be important for overwintering include: (1) generally cool temperatures that minimize the rate of butterfly activity and rate of body fat utilization (Chaplin & Wells 1982, Masters et al. 1988, Alonso-Mejia et al. 1997), (2) a pattern of daily minimum temperature that reduces the likelihood of lethal freezing (Alonso-Mejia et al. 1997), (3) enough moisture to minimize desiccation (Calvert & Lawton 1993), (4) low wind velocity to minimize disruption and desiccation (Leong et al. 1991), and (5) exposure of butterflies in cluster formations to brief mosaics of direct solar radiation to enable periodic thermoregulatory basking (Calvert & Brower 1986, Frey et al. 1992).

Overwintering at Mexico sites occurs during the regional dry season but dehydrating conditions are reduced somewhat because these sites occur at high elevations (2400 to 3600 m) where cloud forests provide relatively high humidity and closed-canopy forests result in wind abatement (Calvert & Brower 1986).

Overwintering at California sites on the other hand occurs during the wet season, yet desiccation is a problem for monarchs. Moisture-producing storms decrease in frequency during February and March, occur sporadically, last for only brief periods and are often followed by many days of dry conditions. For example, during the wet 1998 El Niño event, on 58 days in January, February and March, moisture loss through evapotranspiration exceeded moisture gain from precipitation along the central coast of California (data source: California Department of Water Resources, California Irrigation Management Information System from weather stations located in Guadalupe, California). This potential for desiccation was even more pronounced during the dry 1999 La Niña winter.

An intense period of mating occurs between late January and early March at both Mexico and California overwintering sites during which males compete vigorously for mating opportunities (Hill et al. 1976, Tuskes & Brower 1978, Van Hook 1996, Frey et al. 1998). During a lengthy copulation the male transfers a spermatophore to his partner's reproductive tract, which may equal 10% of his body weight (Oberhauser 1988). Monarch spermatophores contain a small ampoule of spermatozoa along with various nutrients, but consists primarily of water (up to 93%) and females may use this “transferred” water for somatic maintenance (Oberhauser 1992, Pham 1997). At California overwintering sites mating could increase water deficit for males due to the high water content of spermatophores and the seasonal increase in evapotranspiration, solar radiation and temperature. Overwintering sites in Mexico and California are usually associated with a nearby source of water (Calvert & Brower 1986,

Leong 1990, Leong et al. 1991, Bell et al. 1993), but cause and effect relations of monarch hydration activity are not fully understood and hydration behavior has not been studied relative to male mating strategy.

At central coast sites in California monarchs remain relatively inactive throughout much of the overwintering period and spend most of the time in cluster formations (Hill et al. 1976, Tuskes & Brower 1978, Frey & Leong 1993, Frey et al. 1998). On relatively clear days when temperatures exceed the flight threshold many butterflies leave the aggregations and engage in a variety of activities. The majority of them land on sun-exposed canopy vegetation, while some nectar on the limited nearby flowering plants. At the North Beach Campground overwintering site located in Pismo Beach, California many of the butterflies that emerge from aggregations in the early morning fly to an adjacent meadow where they land on dew covered grass and appear to drink from dew droplets (pers. obs.). Small meadows regularly occur adjacent to western North America winter habitat or within the small gaps found in the stand of trees comprising the habitat.

In this study we examined the early morning activity of monarch butterflies at a central coast California overwintering site during the mass mating phase (January through March) of 1998 and 1999. Our objectives were to (1) describe the departure pattern of males and females as they left aggregations to visit a nearby meadow, (2) compare moisture content and morphology of males that visited the meadow to those that remained in aggregations or were engaged in other activities, (3) test whether weather variables from either the current day or from the previous day could explain any patterns from objectives 1 and 2 above, and (4) contrast meadow visiting activity and moisture content during two seasons differing greatly in regional moisture regimes.

#### MATERIALS AND METHODS

**The overwintering site.** This study was carried out in the southeast corner of North Beach Campground, Pismo Beach State Park, Pismo Beach, California. Throughout the study monarchs formed overwintering aggregations in a stand of trees dominated by blue gum eucalyptus (*Eucalyptus globulus* Labill.) along with scattered Monterey cypress (*Cupressus macrocarpa* Hartw.) and Monterey pine (*Pinus radiata* Don). A meadow 60 × 90 m, bordered on the west and north by trees, occurs in the southeast quarter of the site and is comprised primarily of rip-gut brome (*Bromus diandrus* Roth) and veldt grass (*Ehrharta calycina* Smith). The old-growth grass in the meadow was cut back to short stubble in early October during

both years. By the end of March 1998, the grass was 30 to 40 cm tall and uniformly covered most of the meadow. At the end of the overwintering period in the second year, i.e., March 1999, the grass was 20 to 30 cm tall.

**Counts of monarchs in the meadow.** Four uniformly spaced east-west transects were established across the meadow covering a total length of 240 m. On 17 days between 21 January 1998 and 10 March 1998 we visited the site in the early morning before ambient temperature exceeded the flight threshold (10–16°C; Masters et al. 1988, Alonso-Mejia et al. 1993). In 1999 we made 29 morning counts between 28 January and 26 March. On each of these days dew was present on the grass and other meadow vegetation. We slowly walked along each transect and counted the number of male and female monarchs located within 3 m on either side. A second count was done approximately 45 min after the first monarchs began flying out from the cluster trees and landing in the meadow.

**Macro and micro weather conditions.** Pismo Beach is located in a Mediterranean type ecoregion (Bailey 1978) and the study was conducted during what is usually the transition from the wet season to the dry season. The first year of the study occurred during El Niño weather (wetter than average) while the second season was considered a La Niña period (drier than average). For each day of the study we downloaded weather data from nearby California Irrigation Management Information System (CIMIS) recording stations located in Guadalupe and San Luis Obispo, California. The Pismo Beach overwintering site is located between these stations approximately 19 km from each station. The precipitation for January through March in 1998 and 1999 was approximately 50% greater (1998) and 15% less (1999) than the regional 30-year rainfall average. We restricted our observations to rain-free mornings because monarchs do not fly during overcast rainy periods. Year-to-year differences for all other weather variables on days of data collection were not as pronounced as the differences in the overall regional precipitation patterns reported above. In fact, evapotranspiration, solar radiation, and average wind speed recorded at the nearby CIMIS weather stations on days before morning meadow counts did not differ significantly between years (Table 1). We also recorded on-site air temperature in the meadow each day at the time when we observed the initial flight of a monarch from the cluster trees to the meadow and at the time of both of the counts of butterflies along the meadow transect. Initial flight temperature did not differ between years but



TABLE 1. Regional weather variables recorded during 1998 and 1999 on (a) the morning of meadow counts and (b) the day preceding meadow counts. Values are daily means  $\pm$  SE (standard error).

| Variable <sup>1</sup>                   | 1998           | 1999           | P <sup>2</sup> |
|---|----------------|----------------|----------------|
| (a) Temperature of initial flight (°C)  | 11.2 $\pm$ 0.4 | 10.4 $\pm$ 0.3 | 0.106          |
| Change in temperature (°C) <sup>3</sup> | 2.2 $\pm$ 0.4  | 4.4 $\pm$ 0.4  | < 0.001        |
| (b) Evapotranspiration (mm)             | 1.9 $\pm$ 0.3  | 2.2 $\pm$ 0.2  | 0.459          |
| Solar radiation (W m <sup>-2</sup> )    | 144 $\pm$ 17   | 162 $\pm$ 10   | 0.649          |
| Wind velocity (ms <sup>-1</sup> )       | 2.7 $\pm$ 0.2  | 2.5 $\pm$ 0.1  | 0.344          |

<sup>1</sup> Evapotranspiration, solar radiation, and wind velocity values were down-loaded from CIMIS data bases for stations #52 in San Luis Obispo, California and #120 in Guadalupe, California maintained by the California Department of Water Resources.

<sup>2</sup> P-values are from Mann-Whitney tests.

<sup>3</sup> Change in temperature was recorded daily on-site as the difference in temperature of the initial morning flight from cluster trees versus the temperature during the second morning transect count approximately 45 minutes later.

mornings during 1999 warmed more quickly between transect counts than during 1998 (Table 1).

**Moisture content and condition of monarchs.** Males were captured weekly during 1998 from three different categories: (1) dew drinkers: males located in the meadow with their probosces extended into dew droplets on grass, (2) mating pairs: males that had just captured and coupled with a female near the meadow, (3) aggregating individuals: males captured with a net attached to a long-reach pole from the aggregations one hour after ambient temperature exceeded flight threshold. Males from the meadow and those mating were captured immediately following the second transect count of monarchs in the meadow. During 1999, males were captured in the meadow as described for category 1 above on the mornings of 23 February and 2 March. Males were captured from clusters as described for category 3 above on 20 February and 27 February 1999. Mating males were not sampled during 1999.

The number of wings that had membrane tears or portions missing were counted for each butterfly. We placed each male individually in a freezer proof zip-lock bag and stored them in an ice-chest until they were transported to our lab where they were frozen at  $-20^{\circ}\text{C}$ . These specimens were later weighed (wet weight) and then dehydrated in a drying oven at  $60^{\circ}\text{C}$  for 40 h. Individuals were weighed immediately on removal from the freezer to minimize bias due to accumulation of water that condenses on thawing specimens. Following dehydration their dried body weight was recorded and moisture content was estimated as the difference between wet and dry weight. Following dry weight measurement, the abdomen was severed

from the rest of the body and weighed separately. Dry weight of the abdomen relative to total dry body weight was used as an index of body condition or an approximate “fat-content” index.

**Estimation of male mating effort.** We estimated male mating effort in two ways. In the first technique we videotaped courtship responses of males to pinned monarch specimens positioned on platforms in areas of high mating activity. From late morning recording sessions (55 min duration) we summed the number of “visits” by males to the models as well as the number of times males landed on them and tried to couple with the models. For more details of this approach see Falco (1999). These values were converted to standard normal scores and used as an index of population-level male mating effort. The second technique involved late morning counts (approximately 1 h duration) of “ground pairs”, i.e., a male attempting to couple with a female, in the area where mating attempts frequently occurred. We followed the protocol of Frey (1999) and converted the number of observed attempts per minute to standard normal scores.

RESULTS

**Entry rates into the meadow.** A few monarchs were occasionally found in the meadow during count #1 before the beginning of morning flight activity. They were usually wet with dew, much more so than ones collected later in the day, and females were often found near males. We used an abdominal palpation technique (Van Hook 1999) and found that most of the females had a large detectable spermatophore present. This suggested that they had mated recently and possibly had spent part of the previous night in copula in the meadow rather than more typically being attached to males that perched in the canopy of nearby trees.

During the first year of the study the Pismo Beach monarch population declined from a peak abundance of 125,000 butterflies in late December 1997 to less than 1000 individuals by March 1998. During the second year the population declined from 100,000 monarchs in December 1998 to less than 1000 butterflies in March 1999. In both years the sex ratio became increasingly male biased seasonally which is a pattern previously reported for this site (Frey & Leong 1993, 1995, Frey et al. 1998). We computed an index of sex-specific increase in meadow abundance to adjust for the following factors: (1) differences in abundance and sex ratio pattern between years, (2) seasonal declines in abundance due to dispersal that began in January each year, and (3) slight day-to-day differences in the time interval between transect counts. This index was computed by dividing the number of new butterflies

TABLE 2. Number of male and female monarchs counted along transects in a meadow adjacent to overwintering cluster-trees, sex ratios, and per capita meadow entry rate for each sex. Results include 17 and 29 sampling dates for 1998 and 1999 respectively.

| Year | Sex    | First count         | Second count         | Meadow entry rate*         |
|------|--------|---------------------|----------------------|----------------------------|
| 1998 | Male   | 12.6 ± 2.4<br>(67%) | 66.1 ± 12.3<br>(85%) | 0.031 <sup>a</sup> ± 0.006 |
|      | Female | 4.9 ± 1.1<br>(33%)  | 10.6 ± 1.9<br>(15%)  | 0.007 <sup>b</sup> ± 0.004 |
| 1999 | Male   | 2.0 ± 0.6<br>(65%)  | 24.3 ± 2.3<br>(86%)  | 0.023 <sup>a</sup> ± 0.003 |
|      | Female | 1.0 ± 0.3<br>(35%)  | 4.1 ± 0.7<br>(14%)   | 0.011 <sup>b</sup> ± 0.003 |

\* Individuals entering the meadow per min per 1000 males or females remaining in the overwintering area; values with the same letter subscript do not differ significantly ( $P > 0.05$ ) by unpaired Mann-Whitney  $U$ -tests. Counts are means ± SE.

arriving along the transects (i.e., second transect count minus initial count) by the time between counts and then dividing this value by the number of either males or females estimated to be present at the overwintering site on a particular date. Population abundance for each sex were available from MRR Jolly-Seber census estimates made weekly throughout both years of the study (DF unpublished data).

Meadow use rate adjusted for the factors above (i.e., per capita meadow entry) did not differ significantly between years for either sex (Table 2: males,  $P = 0.47$ ; females,  $P = 0.16$ ), but male rate was significantly greater than female rate for both years (Table 2: 1998,  $P < 0.01$ ; 1999,  $P < 0.01$ ). In 1998 male per capita entry rate into the meadow, averaged over the season, was 4.4 times greater than female rate and 2.1 times greater in 1999; by mid-morning the meadow was dominated by males.

**Body moisture, morphology and wing condition of males.** Meadow-captured males had greater moisture content than aggregating males during both years (Table 3:  $P < 0.01$ ) but year-to-year differences in moisture content were not significant (Table 3:  $P = 0.79$ ). During 1998, moisture content for both males collected from the meadow and those captured while mating early in the morning were significantly greater than cluster captured males (1-factor ANOVA & Fisher PLSD test,  $F = 13.57$ ,  $df = 2$ , 135,  $P < 0.01$ ). Males captured after spending less than 1 h in the meadow had approximately 6.7% greater moisture content than their counterparts collected from aggregations.

Males captured from dew-covered grass had significantly less dry weight body mass than cluster-captured males during both years (Table 3:  $P < 0.01$ ). However, a significant two-way interaction effect suggested that

TABLE 3. Moisture content, total dry body mass, and relative abdomen mass of male monarchs. Letters that differ within columns indicate significant differences ( $P < 0.05$ ) by pair-wise Mann-Whitney tests within years.

| Year | Capture category | Sample size | Mean moisture content (%) | Mean dry body mass | Mean dry abdomen mass |
|------|------------------|-------------|---------------------------|--------------------|-----------------------|
|      |                  |             |                           | (mg)               | (%)                   |
| 1998 | Meadow           | 41          | 60 <sup>a</sup>           | 198 <sup>a</sup>   | 28 <sup>a</sup>       |
|      | Aggregations     | 47          | 56 <sup>b</sup>           | 243 <sup>b</sup>   | 30 <sup>b</sup>       |
|      | Mating           | 50          | 59 <sup>a</sup>           | 198 <sup>a</sup>   | 29 <sup>a</sup>       |
| 1999 | Meadow           | 40          | 61 <sup>a</sup>           | 184 <sup>c</sup>   | 35 <sup>c</sup>       |
|      | Aggregations     | 41          | 57 <sup>b</sup>           | 253 <sup>d</sup>   | 43 <sup>d</sup>       |

the difference between dew-drinking vs. clustering male dry mass was more pronounced during 1999 (Table 3: year × category,  $F = 11.49$ ,  $df = 1$ , 165,  $P < 0.01$ ). Meadow-males had 18.5% and 27.3% less dry mass than their clustering counterparts in 1998 and 1999 respectively.

Difference in relative abdomen mass (i.e., dry abdomen mass divided by dry body mass) among the three categories was marginally significant for 1998 (Kruskal-Wallis  $H = 5.6$ ,  $P = 0.059$ ) but field captured males had significantly smaller abdomens than cluster-captured males (Table 3:  $P = 0.019$ ). Meadow-males had significantly smaller abdomens than cluster-males in 1999 (Table 3:  $P < 0.01$ ).

The dew drinking and mating males also had more damaged wings than males taken from clusters during the first year of the study (Two way contingency analysis; 3 groups × 5 damage categories;  $X^2 = 19.6$ ;  $df = 8$ ;  $P = 0.012$ ). Wing damage pattern was not surveyed during year 2.

**Factors affecting meadow use.** Neither the variation in the temperature of initial morning flights nor the variation in the increase in morning temperatures were significantly associated with meadow entry rates for either sex (Table 4). On the other hand, regional solar radiation received during the previous day was significantly associated with meadow entry rate for both sexes (Table 4: males,  $P < 0.01$ ; females,  $P < 0.05$ ). Evapotranspiration and wind velocity were marginal predictors of male meadow use but not female use. Days with dehydrating conditions (high solar radiation, evapotranspiration, and wind velocity) were followed the next morning by high meadow entry rate.

“Mating effort”, i.e., the standard normal scores of the methods outlined above, was significantly associated with male per capita meadow-use or dew-drinking recorded the following morning (Spearman  $Z = 1.95$ ;  $N = 20$ ,  $P = 0.05$ ). When mating activity was high, early morning use of the meadow was high on



TABLE 4. Results of Spearman correlation tests of weather variables as predictors of meadow entry rate during the 46 sampling dates of the 1998 and 1999 monarch mating seasons combined; (a) tests based on temperatures recorded on-site during the morning of meadow counts as predictor variables, (b) tests based on weather conditions during the day preceding meadow counts as predictors.

| Predictor variable |   | Influence on male meadow entry rate |       | Influence on female meadow entry rate |       |
|--------------------|---|-------------------------------------|-------|---------------------------------------|-------|
|                    |   | Spearman "z"                        | P     | Spearman "z"                          | P     |
| (a)                | Temperature of initial flights (°C)       | -1.47                               | 0.142 | -0.87                                 | 0.386 |
|                    | Change in temperature during morning (°C) | 1.58                                | 0.114 | 1.66                                  | 0.097 |
| (b)                | Evapotranspiration (mm)                   | 1.92                                | 0.055 | 1.41                                  | 0.159 |
|                    | Solar radiation (W m <sup>-2</sup> )      | 2.85                                | 0.004 | 2.34                                  | 0.019 |
|                    | Wind velocity (m s <sup>-1</sup> )        | 1.74                                | 0.082 | 0.561                                 | 0.576 |

the following day and vice versa. Female meadow-use was unrelated to the previous day's mating effort (Spearman Z = 0.19; N = 20, P = 0.85).

Female per capita use of the meadow did not change significantly during the course of the season (Spearman correlation; Z = 1.36, P = 0.18, N = 46). On the other hand, male per capita entry into the meadow increased significantly as the mass mating season progressed (Spearman correlation; Z = 2.80, P = 0.005, N = 46). Relatively greater proportions of the male population made early morning visits to the meadow later in the season.

DISCUSSION

Male and female monarchs flew from overnight roosting aggregations to a nearby meadow as morning temperature warmed above the flight threshold. Individuals of both sexes were observed drinking from dew droplets on grass blades, i.e., they had their probosces extended into the droplets for long periods of time. Males collected from the meadow had 6.7% greater moisture content than males collected from aggregations, which also suggests that they had been drinking. Leong et al. (1992) reported monarch water loss between 6% and 10% per day when held without water under lab conditions (19.1°C and 44.9% relative humidity). Males were much more likely to visit the meadow than females during the early morning when dew was available (Table 2).

Dew-drinking patterns were similar between the two years of this study even though the amount of precipitation differed greatly (Table 2). This pattern indicates that monarch moisture levels are closely regulated and influenced more by short-term events (e.g., the past 24 to 48 h) than over a longer term. In contrast, year-to-year differences in relative abdomen mass (Table 3, larger abdomens in 1999) probably reflected overall differences in temperature regimes between El Niño and La Niña seasons and the fact that fat reserves are used more rapidly under higher temperatures (Chaplin & Wells 1982). Average daily tem-

perature during January, February, and March of 1998 approximated the 30-average for the Pismo Beach area but were 4%, 3%, and 9% below normal respectively during 1999.

There are several reasons why water may be particularly important to males during the mass mating period at overwintering sites beyond a general need to reduce negative systemic physiological effects that may accompany desiccation. Three hypotheses regarding early morning dew-drinking are given in Table 5 along with specific testable predictions for each hypothesis. Early morning temperatures could influence flights from cluster trees (Table 5, Current Weather-hypothesis 1) because flight thresholds can vary slightly among individuals in overwintering populations (Masters et al. 1988, Anson Lui pers. com.). Alternatively, or in addition, weather associated with dehydration during the previous day could influence dew-drinking on the following morning (Table 5, Previous Day Weather-hypothesis 2). To test these first two hypotheses we combined data from both years of the study for the following three reasons: (1) per capita meadow entry rate did not differ between years for either sex (Table 2), (2) on-site temperature during the initial morning flights did not differ between years, and (3) the regional evapotranspiration, solar radiation, and wind velocity on days preceding our observations of dew-drinking did not differ between the two years (Table 1).

Neither temperature-related prediction of the "current weather constraint" hypothesis, i.e., Table 5-hypothesis 1, was borne out in this study (Table 2 & Table 4a). Early morning conditions, however, can influence meadow use since monarchs are constrained from flying at temperatures below approximately 10°C and they seldom fly under overcast conditions (pers. obs.). One of the two predictions of the "previous day weather" hypothesis, i.e., Table 5-hypothesis 2, was confirmed. Levels of solar radiation and other weather variables associated with dehydration on a given day were positively correlated with dew-drinking rate on

TABLE 5. Three hypotheses regarding monarch butterfly early morning dew-drinking.

| Hypothesis                       | Description  | Predictions  |
|----------------------------------|--|--|
| (1) Current weather constraint   | Flight from overnight cluster aggregations is constrained by low temperatures (Masters et al. 1988), thus variation in morning temperature influences early morning meadow visits. | 1. Meadow use should be greater on mornings that warm more quickly.<br>2. Male and female pattern should be similar  |
| (2) Previous day weather         | Weather conditions associated with dehydration (e.g., evapo-transpiration) during the previous day influence dew-drinking on the following morning.                                | 1. Days with high levels of evapo-transpiration, wind velocity, and solar radiation should be followed by mornings with high levels of dew-drinking and vice versa.<br>2. Male and female pattern of dew use should be similar   |
| (3) Previous day mating activity | High levels of mating activity increase dehydration among monarchs and should influence dew-drinking on the following morning.   | 1. Measures of mating effort at the population level should correlate with dew-drinking rate on the following morning.<br>2. Males should be more strongly affected than females.<br>3. Per capita dew-drinking rate should increase seasonally for males but not for females. |

the following morning, but the effect was much more pronounced for males than females (Table 4b).

A third hypothesis that may account for the dew-drinking pattern reported here relates to the level of mating activity on the previous day (Table 5—hypothesis 3). Similar to other butterflies, monarch mating consists of several stages (Rutowski 1991). Initially males locate potential partners either by perching on sun-exposed vegetation and waiting for females to pass nearby or by patrolling the air space near roosting trees (Falco 1999). Both of these locating tactics expose males to direct sunlight, dry air, and high wind speeds. These conditions are more dehydrating than if they remained clustered. Early morning dew drinking by males and females may be a direct response to water deficit incurred primarily during mating effort on the previous day.

Water uptake by male monarchs may influence their reproductive success indirectly. The majority of females mate multiple times at California overwintering sites (Hill et al. 1976, Leong et al. 1995, Frey et al. 1998, Frey 1999). A pattern of sperm precedence exists so that sperm from the most recent mating fertilizes the majority of eggs (Karen Oberhauser pers. com.) and sperm can survive for several weeks (Oberhauser 1997). A male's reproductive success is probably a function of his partner's subsequent inter-mating interval. Females that receive relatively large spermatophores have longer inter-mating intervals (Oberhauser 1989) and are more likely to exhibit effective resistance to male mating attempts (Frey 1999). Early morning dew drinking may enable males to generate accessory fluids necessary to produce a relatively large spermatophore during a subsequent mating and thus indirectly reduce chances that his sperm will be displaced. It is possible that dew drinking in this case is

also strategic behavior rather than a simple response to water deficit. All three predictions of the "previous day mating activity" hypothesis, i.e., Table 5—hypothesis 3, were supported by our findings (see Results—Factors affecting meadow use).

Males that visited the meadow exhibited morphometric characters that were more similar to early morning mating-pool individuals than those captured later during the morning from clusters. Dew-drinking males had lower body weight (dry-mass), smaller abdomens, and higher wing damage (Table 3). Male monarchs attempting to mate differed similarly from clustering males at Mexico and California overwintering sites (Van Hook 1996, Frey et al. 1998, Oberhauser & Frey 1999). Both dew-drinking and mating males in our study had relatively high moisture content (Table 3). Sunny, drier, and windier days were followed by increased male dew drinking the next morning (Table 4). In addition per capita dew drinking increased seasonally for males (but not for females) and their per capita mating effort also has been found to increase seasonally at this site (Falco 1999, Frey 1999). This is an expected pattern if water "lost" by males, both from increased exposure to desiccation during mating attempts as well as during spermatophore transfer, was replenished by dew drinking. On the other hand, many of the meadow-visiting males attempted to capture females within minutes of drinking dew. This is consistent with the view that early-morning dew drinking is a strategic male activity with the potential to increase short-term reproductive success in the ways described above.

Male-biased sex ratios similar to those reported here for dew-drinking are described for puddling activity in other Lepidoptera (Adler 1982, Adler & Pearson 1982, Boggs & Jackson 1991, Sculley & Boggs 1996, Beck et



al. 1999; but see Scriber 1987). Puddling is often viewed as differential foraging, which either supplies ionic or nutrient resources needed by males (Arms et al. 1974) or is a means for males to acquire resources that they transfer to females during copulation (Sculley & Boggs 1996). Alternatively, or in addition, male biased puddling in Lepidoptera could provide moisture for reproductive activities, as well as, maintenance, as outlined above for monarchs. Monarchs also puddle at Mexico overwintering sites (pers. obs.) but puddling has not been reported for monarchs in western North America.

Nectaring from nearby flowering plants has been observed for monarchs during the mass mating phase at a Mexico overwintering site (Alonso-Mejia et al. 1997). Flower-visiting monarchs in Mexico were smaller (dry mass), had significantly less fat reserves and had relatively greater moisture levels than cluster-captured ones (58% vs. 54% respectively for moisture as a proportion of wet body weight; our calculations of data from Table 2 in Alonso-Mejia et al. 1997). The pattern for moisture content of these Mexico monarchs is similar to those from our dew-drinking study and indicates that nectaring can also provide monarchs with a source of water. Few nectar sources however occur near the Pismo overwintering habitat and monarchs are seldom observed nectaring during January and February (pers. obs.). Likewise, they seldom drink from open water that usually occurs in shaded areas of the habitat, suggesting that monarchs probably obtain most of their water from dew or water droplets.

Dew drinking by monarchs, like nectaring and puddling, may be "triggered" by a number of proximate-level factors and may provide water that is used in several functional contexts. Early morning dew drinking by monarchs seems to be a response to short-term dehydration as well as strategic behavior associated with male reproductive activity.

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#### LITERATURE CITED

ADLER, P. 1982. Soil- and puddle-visiting habits of moths. *J. Lepid. Soc.* 36:161–173.  
 ADLER, P. & D. PEARSON. 1982. Why do male butterflies visit mud puddles? *Canadian J. of Zool.* 60:322–325.  
 ALONSO-MEJIA, A., J. GLENDINNINC & L. BROWER. 1993. The influ-

ence of temperature on crawling, shivering, and flying in overwintering monarch butterflies in Mexico, pp. 309–314. *In* S. Malcolm & M. Zalucki (eds.), *Biology and conservation of the monarch butterfly*. Los Angeles, Science Series No. 83, Natural History Museum of Los Angeles County.  
 ALONSO-MEJIA, A., E. RENDON-SALINAS, E. MONTESINOS-PATINO & L. BROWER. 1997. Use of lipid reserves by monarch butterflies overwintering in Mexico: implications for conservation. *Ecol. Applic.* 7:934–947.  
 ARMS, K., P. FEENY & R. LEDERHOUSE. 1974. Sodium: stimulus for puddling behaviour by tiger swallowtail butterflies. *Science* 185:372–374.  
 BAILEY, R. 1978. Descriptions of the ecoregions of the United States. U.S.D.A. Forest Service Intermountain Region, Ogden Utah.  
 BECK, J., E. MUHLENBERG & K. FIEDLER. 1999. Mud-puddling behavior in tropical butterflies: in search of proteins or minerals? *Oecologia* 119:140–148.  
 BELL, E., L. BROWER, W. CALVERT, J. DAYTON, D. FREY, K. LEONG, D. MURPHY, R. PYLE, K. SNOW & S. WEISS. 1993. The monarch project's conservation and management guidelines for preserving the monarch butterfly migration and monarch overwintering habitat in California. Portland, Xerces Society publications.  
 BOCCS, C. & L. JACKSON. 1991. Mud puddling by butterflies is not a simple matter. *Ecol. Entomol.* 16:123–127.  
 BROWER, L., W. CALVERT, L. HEDRICK & J. CHRISTIAN. 1977. Biological observations on an overwintering colony of monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico. *J. Lepid. Soc.* 31:232–242.  
 BROWER, L. & S. MALCOLM. 1991. Animal migrations: endangered phenomena. *Amer. Zool.* 31:265–276.  
 BROWER, L. P. 1985. New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L., pp. 748–785. *In* M. A. Rankin (ed.), *Migration: mechanisms and adaptive significance*. University of Texas, Austin, Texas.  
 CALVERT, W. & L. BROWER. 1986. The location of monarch butterfly (*Danaus plexippus* L.) overwintering colonies in Mexico in relation to topography and climate. *J. Lepid. Soc.* 40:164–187.  
 CALVERT, W. & R. LAWTON. 1993. Comparative phenology of variation in size, weight, and water content of eastern North American monarch butterflies at five overwintering sites in Mexico, pp. 299–307. *In* S. Malcolm & M. Zalucki (eds.), *Biology and conservation of the monarch butterfly*. Los Angeles: Science Series No. 83, Natural History Museum of Los Angeles County.  
 CALVERT, W., W. ZUCHOWSKI & L. BROWER. 1982. The impact of forest thinning on microclimate in monarch butterfly (*Danaus plexippus* L.) overwintering sites in Mexico. *Boletín de la Sociedad Botánica de México* 42:11–18.  
 CHAPLIN, S. & P. WELLS. 1982. Energy reserves and metabolic expenditures of monarch butterflies overwintering in southern California. *Ecol. Entomol.* 7:249–256.  
 FALCO, L. 1999. Variation in male courtship behaviors of the monarch butterfly (*Danaus plexippus* L.) at central California overwintering sites. M.S. Thesis, California Polytechnic State University.  
 FREY, D. 1999. Resistance to mating by female monarch butterflies, pp. 79–87. *In* J. Hoth, L. Merino, K. Oberhauser, I. Pisanty, S. Price & T. Wilkinson (eds.), 1997 North American Conference on the Monarch Butterfly. Commission for Environmental Cooperation, Montreal.  
 FREY, D. & K. LEONG. 1993. Can microhabitat selection or differences in 'catchability' explain male-biased sex ratios in overwintering populations of monarch butterflies? *Anim. Behav.* 45:1025–1027.  
 ———. 1995. Reply to Nylin, Wickman & Wiklund regarding sex ratios of California overwintering monarch butterflies. *Anim. Behav.* 49:515–518.  
 FREY, D., K. LEONG, D. FREDERICKS & S. RASKOWITZ. 1992. Cluster patterns of monarch butterflies (*Danaus plexippus* (L.)

- Danaidae: Lepidoptera) at two central California coast overwintering sites. *Ann. Entomol. Soc. Am.* 85:149–153.
- FREY, D., K. LEONG, E. PEFFER, R. SMIDT & K. OBERHAUSER. 1998. Mate pairing patterns of monarch butterflies (*Danaus plexippus* L.) at a California overwintering site. *J. Lepid. Soc.* 52:84–97.
- HILL, H., A. WENNER & P. WELLS. 1976. Reproductive behavior in an overwintering aggregation of monarch butterflies. *Am. Midl. Nat.* 95:10–19.
- LANE, J. 1993. Overwintering monarch butterflies in California: past and present, pp. 335–344. In S. Malcolm & M. Zalucki (eds.), *Biology and conservation of the monarch butterfly*. Los Angeles: Science Series No. 83, Natural History Museum of Los Angeles County.
- LEONG, K. 1990. Microenvironmental factors associated with the winter habitat of the monarch butterfly (Lepidoptera: Danaidae) in central California. *Ann. Entomol. Soc. Am.* 83:907–910.
- LEONG, K., D. FREY, G. BRENNER, S. BAKER & D. FOX. 1991. Use of multivariate analyses to characterize the monarch butterfly (Lepidoptera: Danaidae) winter habitat. *Ann. Entomol. Soc. Am.* 84:263–267.
- LEONG, K., H. KAYA, M. YOSHIMURA & D. FREY. 1992. The occurrence and effect of a protozoan parasite, *Ophryocystis elektroscirrha* (Neogregarinida: Ophryocystidae) on overwintering monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae) from two California winter sites. *Ecol. Entomol.* 17:338–342.
- LEONG, K., E. O'BRIEN, K. LOWERISEN & M. COLLERAN. 1995. Mating activity and status of overwintering monarch butterflies (Lepidoptera: Danaidae) in central California. *Ann. Entomol. Soc. Am.* 88:45–50.
- MASTERS, A., S. MALCOLM & L. BROWER. 1988. Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. *Ecology* 69:458–467.
- OBERHAUSER, K. 1988. Male monarch butterfly spermatophore mass and mating strategies. *Anim. Behav.* 36:1384–1388.
- . 1989. Effects of spermatophores on male and female monarch butterfly reproductive success. *Behav. Ecol. Sociobiol.* 25:237–246.
- . 1992. Rate of ejaculate breakdown and intermating intervals in monarch butterflies. *Behav. Ecol. Sociobiol.* 31:367–373.
- . 1997. Fecundity, lifespan and egg mass in butterflies: effects of male-derived nutrients and female size. *Functional Ecol.* 11:166–175.
- OBERHAUSER, K. & D. FREY. 1999. Coercive mating by overwintering male monarch butterflies, pp. 67–78. In J. Hoth, L. Merino, K. Oberhauser, I. Pisanty, S. Price & T. Wilkinson (eds.), 1997 North American Conference on the Monarch Butterfly. Commission for Environmental Cooperation, Montreal.
- PHAM, E. 1997. Chemical composition of the spermatophores of overwintering monarch butterflies (*Danaus plexippus* (L.)). M.S. Thesis, California Polytechnic State University. 41 pp.
- RUTOWSKI, R. 1991. The evolution of male mate-locating behavior in butterflies. *The Amer. Natur.* 138:1121–1139.
- SAKAI, W. & W. CALVERT. 1991. Statewide monarch butterfly management plan for the state of California Department of Parks and Recreation. Final Report for California Department of Parks and Recreation.
- SCRIBER, J. 1987. Puddling by female Florida tiger swallowtail butterflies, *Papilio glaucus austoralis* (Lepidoptera: Papilionidae). *The Great Lakes Entomologist* 20:21–23.
- SCULLEY, C. & C. BOGGS. 1996. Mating systems and sexual division of foraging effort affect puddling behaviour by butterflies. *Ecol. Entomol.* 21:193–197.
- TUSKES, P. & L. BROWER. 1978. Overwintering ecology of the monarch butterfly, *Danaus plexippus* (L.), in California. *Ecol. Entomol.* 3:141–153.
- URQUHART, F. & N. URQUHART. 1978. Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae: Lepidoptera) in North America to the overwintering site in the neovolcanic plateau of Mexico. *Can. J. Zool.* 56:1754–1764.
- VAN HOOK, T. 1996. Monarch butterfly mating ecology at a Mexican overwintering site: proximate causes of non-random mating. Ph.D. Dissertation, University of Florida.
- . 1999. The use of bursa copulatrix dissection and abdominal palpation to assess female monarch butterfly mating status, pp. 101–111. In J. Hoth, L. Merino, K. Oberhauser, I. Pisanty, S. Price & T. Wilkinson (eds.), 1997 North American Conference on the Monarch Butterfly. Commission for Environmental Cooperation, Montreal.

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